

RUBIACEAE

NAME: The family name is from the genus *Rubia*, the Indian Madder, from Latin for red in reference to the dye color extracted from the roots. Many individual species of this family are well known and bear local vernacular names, but no name applies to the family as a whole. In English, the Rubiaceae are rendered as the Coffee family. The large or distinctive genera often have their local own names while small shrubs with axillary fruit are sometimes lumped in Malay as *kopi hutan*.

OVERVIEW: The Rubiaceae are one of the most abundant and species-rich of plant families. They are broadly cosmopolitan in distribution although overwhelmingly tropical and greatly diminished in diversity and abundance north of 20 degrees latitude. The family is strongly monophyletic and relatively easy to recognize. The opposite, shiny leaves with entire margins and a conspicuous stipule pair above or between the leaves signals the family identity and makes the Rubiaceae one of the first families added to the student's vocabulary. Many of the more abundant genera are likewise easily recognizable, and after meeting *Ixora*, *Pavetta*, *Lasiacanthus* and *Nauclea* a student may be tempted to think that they are on their way toward a comprehension of the family. But the first date is deceptive, and the further courtship is a bumpy road of starts and stops. Most forest botanists eventually give up trying to understand the genera, and with good reason. The species and genera are numerous and differ by combinations of fine details of flower and fruit, or are distinguished by features not readily visible in the field - the presence or absence of raphide crystals, the way in which the ovule attaches to the carpel wall, the form of the pollen and seed coat.

The sheer number of names is sufficiently daunting so as to preclude any comprehension of the family's diversity. *Index Kewensis* records over 1500 published genera in the family and more than 30,000 species names. Those are currently thought to represent between 11,000 and 13,000 species. However, the species are still arranged in what seems like an unreasonably divisive 660 genera. Certainly, any student is entitled to ask why the 670 species of Rubiaceae known for Thailand require 110 genera when the 470 species of Dipterocarpaceae in tropical Asia are adequately comprehended in just 11 genera.

The advent of molecular evidence has gifted the family with increasing clarity of organization, and the prospects for a broad comprehension of the family with regard to ecology and geography is within view. The principle findings are summarized in a recent review by Bremer.

Three strong clades are now usually represented as subfamilies: the *Rubia* or *Psychotria* Subfamily (Rubioidae, chiefly shade-loving herbs and soft climbers, raphides present, heterostyly common); the *Cinchona* subfamily (Cinchonoideae, with many large sun-loving trees with dry fruit and winged seeds); and the *Ixora* Subfamily (Ixoroideae, with the bulk of our multi-branched shade-loving shrubs). The latter two subfamilies share the absence of raphides and the possession of secondary pollen presentation. Two eccentric genera (*Luculia*, a genus of Himalayan shrubs, and our scrambling shrub *Coptosapelta*) appear to fall basal to the rest of the family or perhaps to the Cinchonoideae, but they are an odd pair and are best left unplaced pending further data. An alternative two-family arrangement is championed by Robbrecht *et al.*⁵.

The family as a whole can be characterized as herbs, woody climbers, shrubs and small trees, with greater rarity among trees over 10 cm DBH, and only a few species over 30 cm DBH. They bear opposite leaves typically 10-20 cm long with entire margins and a pair of stipules between the leaves, persistent or leaving an obvious scar. The flowers are bisexual, epigynous, typically small 3-6 mm across, clustered in a cyme-like inflorescence but variously modified. They are basically five-merous, but four-merous flowers are almost equally common and have evolved in every major group. The calyx bears small lobes but varies with regard to symmetry and a propensity to unequal size. In contrast, the corolla is fairly uni-

FIELD RECOGNITION: RUBIACEAE

Readily diagnosed by the opposite, entire leaves, pinnately nerved, shortly stalked, with prominent stipules.

The body without exudate but the twig tips sometimes exuded resin.

FIELD CONFUSION

Rhizophoraceae have a similar stipule between the leaf stalks, but the leaf margin is finely serrate.

The same can be said of Chloranthaceae, which also differs in the decidedly swollen node.

Gnetum gnemon is without stipules and bears a decidedly swollen node.

Melastomes lack stipules but do have an inter-petiole scar. Nonetheless, they are readily distinguished by their characteristic venation, or in the case of *Memecylon*, the venation is usually looped or with an intramarginal vein, never found in Rubiaceae.

The peculiar species of Euphorbiaceae in *Erismanthus* look very much like a Rubiaceae owing to the odd small leaflets at the node, but the leaf blade is finely toothed.

Most other opposite-leaved trees have a yellow or white exudate (Apocynaceae) or the blade is strongly palmately nerved.

¹Bremer B. *et al.* 1995. *Annals of the Missouri Botanical Garden*. 82: 383-397.

²Bremer B. *et al.* 1997. *Cladistics*. 12: 21-40.

³Bremer, B. *et al.* 2000. *Plant Systematics and Evolution* 225: 43-72.

⁴Bremer, B. 2009. *Annals of the Missouri Botanical Gardens*. 96: 4-26.

⁵Robbrecht, E. *et al.* 2006. *Systematics and Geography of Plants* 76: 85-146.

form in size, the tube mostly about 5-8 mm long, and only a few species of *Gardenia* relatives bear truly large flowers. The arrangement of petal lobes varies among contorted, valvate and imbricate. The numerical majority of species bear white flowers, but yellow, and red and blue flowers also occur. The stamens attach to corolla tube alternate with lobes. The ovary is characteristically inferior. Exceptions are *Gaertnera* with a fully superior ovary. Carpel number and ovule number and placement vary greatly, and do not decisively define subfamilies or tribes, although they are generally characteristic of some groupings. The fruit most often is a fleshy berry, less commonly a dry dehiscent capsule.

Most of the thousand species of Rubiaceae share a basic vegetative form that allows their ready recognition to family: the leaf stalk is short unswollen and fleshy, the nerves regularly pinnate, the blade glossy, the margin entire. Despite this seeming uniformity, there is a wealth of variation in details of vegetative and floral form. The inflorescence architecture has been especially plastic and includes great terminal panicles or small sphere-like heads, axillary spikes or blunt clusters. The phyllotaxy is fundamentally decussate but architecturally diverse with numerous secondary modifications through twisting, shortened or lengthening of internodes and reduction of one or both leaves. Leaf domatia in the axils of the main nerves on lower leaf surface are common, and although small, are diverse: tufts of hair, pits, and pitted domes.

Rubiaceae are rarely cauliflorous. Some forms of *Ixora pendula* flower from the older branches, and in the Philippines we find a form that is truly cauliflorous. The inflorescence can be congested to various extents and can be reduced to a few flowers, or even one.

The paired stipules that characterize the family serve to protect the growing apex. Often they are fused early in growth as glandular bodies in the leaf stalk axil (inevitably called colleters) produce waxy substance that glues together the young stipules. In some species, especially *Gardenia*, these secretions can be very noticeable. A few species in the *Nauclea*-group have ant-inhabited stems.

Bacterial eaf nodules are obvious in three unrelated genera of the Rubiaceae: the Africa genus *Sericanthe*, most African and Asian species of *Pavetta*, and about 70 African species of the pantropical genus *Psychotria*. The function and benefits to the host are undemonstrated.

The family Rubiaceae comprises one of the ecological foundations of the lower forest strata, a key source of food for birds because they are often in fruit and flower when nothing else is.

Most Asian Rubiaceae have one of two floral syndromes. In the first we find an elongated corolla pollinated by insects or birds with long mouth parts. A second syndrome consists of a short corolla tube and an inflorescence of numerous flowers conspicuous in aggregation, nectariferous and pollinated by various insects. In tropical America we find more than a few bird-pollinated species characterized by long corollas, red in color, sometimes curved. This type is, I believe, at least rare if not unknown in tropical Asia. Flowering rhythms in the Rubiaceae range from synchronous, in which all flowers

of an inflorescence open at once, or long asynchronous, in which flowers of an inflorescence open singly over many days or weeks.

There are more species of Rubiaceae in tropical Asia than in any other family of trees and shrubs, but the seeming success should be cautioned in several respects. The family does not hold its lead in any particular forest, where it usually falls to the third or fourth ranking in number of species. Also, while the family is common it is by no means dominant in number of stems. Furthermore, because these are mostly of small stature, the family comprises a relatively small portion of the total forest biomass.

Considering the species richness of the family, its abundance and ease of cultivation, it is surprising that there are so few members that have been economically exploited. Coffee is the most famous and one of the most lucrative of all legal plant products with annual production of 5-10 million metric tons; the raw fruit alone represents a multi-billion dollar industry with even larger economic impact at the retail level. *Cinchona* was the original source of quinine. *Uncaria*, although scarcely known as an economic product today, was once a major source of gambier for tanning and contributed to the 19th Century clearing of Singapore as the forests were cut to fuel the boiling of the leaves. The family is abundant in cultivated ornamentals: especially our *Ixora*, *Gardenia* and *Mussaenda*. However, there are undoubtedly a great many other species that could be exploited as ornamentals.

The family has advantages that continue to attract stout hearted students unafraid of large numbers. The plants are small and flower regularly such that new collections are easily made and can be added to the relatively large numbers of past collections. Also, a prospective student of the Rubiaceae will find much company - typically enthusiastic and full of strongly held opinions. Keys can be found for most of the individual parts of tropical Asia. Rubiaceae can boast a recent checklist as well as numerous books, a web site for the Rubiaceae of the Philippines and a nice collection of photos for those of Thailand.

☞ - The *Psychotria* Subfamily - ☞ (Rubioideae)

Especially herbs, small trees, multi-branched shrubs, stipules often bifid or fimbriate, raphides often present, corolla lobes mostly valvate, placenta with one or many ovules, seed number variable, fruit variable, heterodistly common.

A - Tribe Gaertnereae - a

GAERTNERA. [Commemorates Joseph Gaertner, German botanist, d. 1791, celebrated author of *De Fructibus et Seminibus Plantarum*.] Some species as *baju-filipino* in Malay from fancied resemblance of the stipular

wings to the butterfly shoulders of the filipino *terno*. The common name in Sarawak is *mengudu* reflecting the similarity with *Morinda*. About 48 species are recognized, from Africa to India to S China and east where it is common throughout the Sundaic Region. They bear dimorphic flowers: short-style/long-stamens and long-style/short-stamens. The eight species of tropical Asia differ from those to the west in that the flowers are unisexual, the plants dioecious, except for unnamed species in North Borneo.

The ovary of these small trees is unlike other Rubiaceae in that it initiates in a half-inferior position then matures as fully superior. In older literature, this genus might be found in the family Loganiaceae, but molecular data confirms their rightful home in the Rubiaceae and recommends a position basal in the *Psychotria* subfamily. The inflorescence is essentially terminal. The stipules are peculiar in one way or another: in many species

they are a long sheathing collar, in others they form an odd flange.

Gaertnera vaginans occurs widely in tropical Asia from the mountains of Thailand and Vietnam to Borneo and beyond. It is a small tree not reaching 10 cm DBH, ecologically and morphologically variable, abundant in secondary forests and *kerangas* in Sarawak. These are currently lumped as a broad species that includes African and Madagascan forms in which the flowers are bisexual and heterostylous, whereas the Sundaic representative are homostylous. A peculiar small tree of the forest understory, *G. oblancoolata*, bears a stout stem and an odd flanged stipule, flowers frequently and would be ideal subject for studies of pollination.

A - Tribe Morindeae - a

MORINDA. [From a combination of *Morus* and India, Indian-mulberry.] 50 species, pantropical. In tropical Asia, these trees are chiefly found in dry-seasonal places with 13 species in Thailand, 10 in Malaya, three as trees. Branches in the tree species are sympodial, flowering after every two nodes; the inflorescence apparently leaf opposed, the subtending leaf not developing, the flowers in heads, the calyx cups fused together creating a fleshy syncarpous structure.



Gaertnera. 1-4, *G. oblancoolata*, Malaya; 1, a small understory tree with terminal inflorescences, dioecious; 2-3, staminate flowers; 4, pistillate flowers; 5-6, *G. villosa*, Singapore, the twig with a conspicuous sheathing stipule; 7, *G. vagrans*, a specimen from Malaya showing the dry leaf, terminal inflorescence and sheathing stipule.

⁶Govaerts, R., *et al.* 2007. World Checklist & Bibliography of Rubiaceae.

⁷Puff, C. *et al.* 2005. Rubiaceae of Thailand: A pictorial guide to indigenous and cultivated genera.

⁸Wong, K. 1990. Tree Flora of Malaya. 4: 324-425.

⁹Alejandro, G. *et al.* 2002. (<http://www.uni-bayreuth.de>).

¹⁰Puff, C. (<http://www.homepage.univie.ac.at>).

Morinda citrifolia is the *mengkudu* in Malay, and internationally known by the Hawaiian name *noni*. It is especially common on old raised beaches, mangroves, riversides and inland on roadsides, secondary habitats, sometimes in casual cultivation. The seeds disperse by seawater, and the tree is all over tropical Asia and the Pacific. At maturity the fruit is yellow, soft and utterly fetid, accurately named *cheese-fruit* by Australians. Unlike most herbal fads, which offer at least some redeeming quality, *noni*-juice combines the utter want of demonstrable benefits with an awful taste, and so naturally has been propelled to international fame.

Morinda elliptica has narrow leaves, fragrant flowers and small black fruit on stalks 2-5 cm long; it is found from Malacca north to Thailand and Myanmar, and is a common part of secondary forests. A different form of this is found in Pahang and Terengganu, *M. corneri*, with nearly sessile fruit closer to blue than black.

Most species bear a dye, red to brown in color, especially in the root of young trees. The genus provided a small but locally important dye industry, especially in India (*M. tinctoria*) at the turn of the century, and to some extent in Java and Malaya, where roots and bark yield dyes of colors preferred for batik.

RENNELIA. [Commemorates James Rennell, d. 1830, English Surveyor for East India Company.] Six species, Sundaic Region, *metemak* (Malaya). Small treelets, especially of Malaya and Borneo, reaching S Thailand, frequent enough to be found in most wet forests. The stipules are sheathing and usually with a split apex. The distinguishing feature is the inflorescence which



Rennellia speciosa, Sarawak; note the knotty white twig, terminal spike of sessile flowers with long floral tubes.



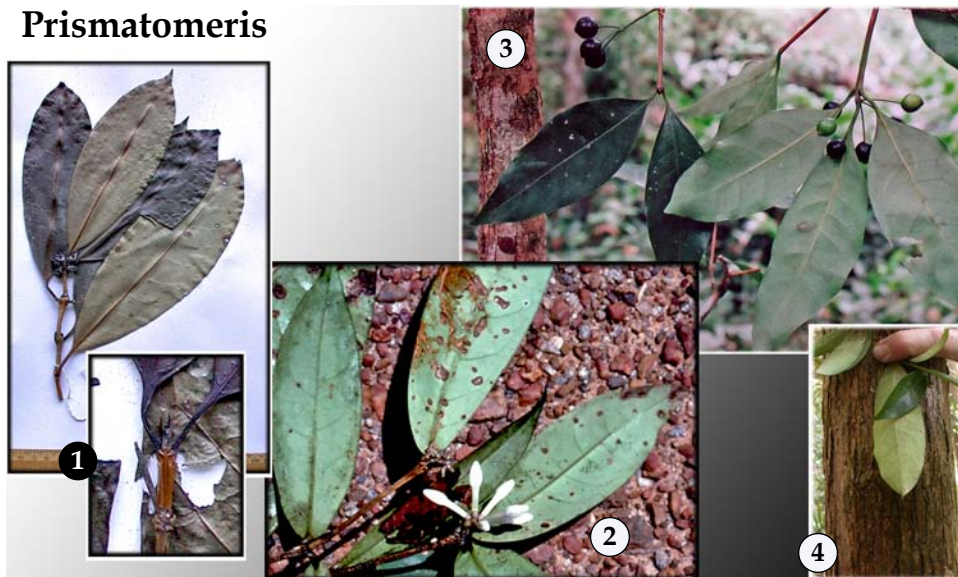
Morinda citrifolia, Philippines, inflorescence and developing fruit; inset of the tree on a sandy beach.

is a terminal spike with the flowers aggregated in clusters, their ovaries fused. They are said to be distylous. The inflorescence varies among species. In *R. elliptica* of the Sundaic Region, the inflorescence is a long spike, while in the Malayan *R. speciosa* the inflorescence is like a umbel, the stalks of the heads are only three-seven mm long; in *R. morindiformis* the stalks of the heads are 12-40 mm long.

PRISMATOMERIS. [Greek, in reference to the sharply cut petal apex.] *Prismatomeris* is a genus of about 15 species exclusively in tropical Asia from India and Sri Lanka to New Guinea and the Philippines. These are small trees and multi-branched shrubs, the largest not exceeding 10 cm DBH, typically with a shredding brown-gray bark. In India, Sri Lanka and Mainland SE Asia, *P. tetrandra* is a widespread and abundant small understory tree of semi-evergreen forests. It bears thick green leaves with weakly raised nerves and obscure veins. In the Sundaic Region, more species of a wider variety of forms are found. Many are thick-leaved like *P. tetrandra*, while a few Bornean species bear thin papery leaves that dry gray-black. Most have pale colored sharply angled and waxy twigs with swollen nodes that give the twigs a knotty appearance. The flowers, which may be technically axillary, are typically clustered at the ultimate nodes. A critical revision of *Prismatomeris* is much needed, especially with regard to the Bornean and Philippine species.

DAMNACANTHUS. [Greek, conquering thorns.] Maybe six species, Palearctic, but probably

Prismatomeris



Prismatomeris. 1, a species from Sarawak, likely new, with swollen nodes, waxy ridged twigs, winged stipules, thick, hard, stiff leaves, all features characteristic of the genus, while the fruit are here nearly sessile and weakly fused, features found in some species; 2, an undescribed species of *Prismatomeris* from Pasoh Forest, Malaya, perhaps related to *P. sessiliflora*; 3, leaves, long stalked fruit and 2 cm DBH stem of *P. tetrandra*, Huai Kha Khaeng, Thailand; 4, leaf and bark of *P. glabra*, Malaya.

only *Damnacanthus indicus* in our region, from India to S China and Japan, south in Myanmar, Laos and Vietnam, evidently not yet for N Thailand, and also from Mt. Banahaw in Luzon, Philippines. These are all small thorny shrubs, Heterophylly and sympodial growth are obvious. The thorns sometimes reach two cm in length. The stipules are small, entire or bifid, the leaves variably in size up to three cm long. The inflorescence is terminal, composed of flowers with parts in fours, actinomorphic, bisexual. The corolla is one–two cm long, fruits fleshy and bright red, the pyrenes without ridges. (Not illustrated.)

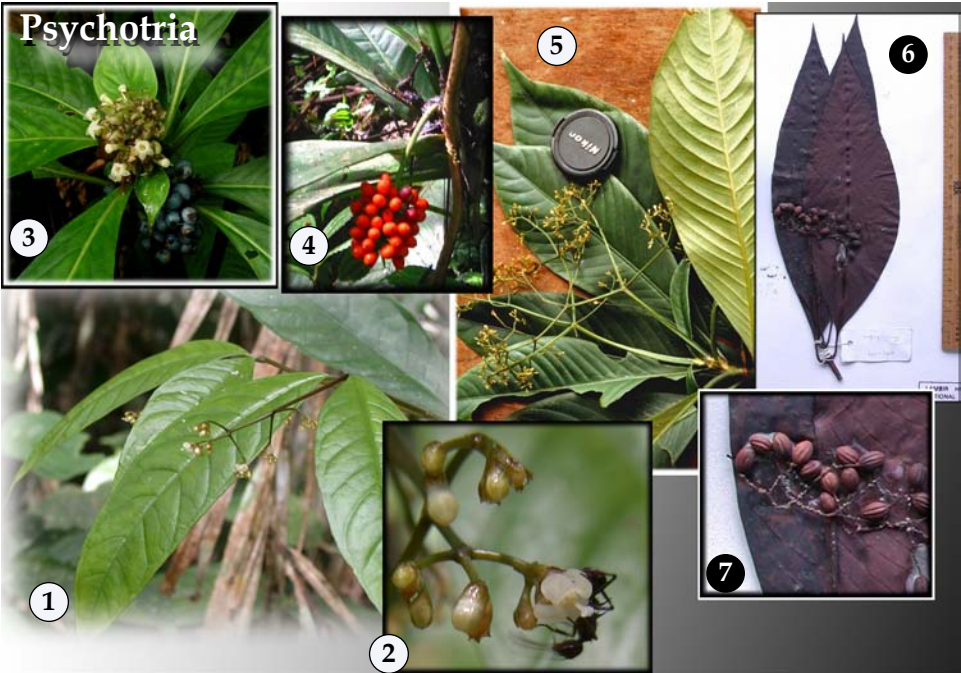
A - Tribe Psychotrieae - a

PSYCHOTRIA. [The name by Linnaeus, a shortened form of an earlier name, *Psychotrophon*, from the Greek for psyche and to support, in reference to supposed medicinal value.] This vast genus is often described as the most species-rich in the world with more than 4700 basionyms representing perhaps 800-1500 species, many known from single locations. It is pantropical in distribution, however the monophyly of the genus is doubtful and the constituent clades are still poorly resolved. Mostly small multi-branched shrubs. The Neotropical forms are far more diverse in form and exhibit an even higher species richness than found in Asia. American examples include types with floral heads and brightly colored bracts formerly called *Cephaelis*; however, while we have a few species formerly in *Cephaelis*, the bracts are never so large and showy as the American types. Nevertheless, the Asian *Psychotria* are also heterogeneous in

most features especially the stipule which, while often two-lobed or triangular can be of almost any other sort. Most of our species bear many small flowers in terminal inflorescences that is variably condensed; the fruit is two-seeded and usually distinguished when dry by the strong ribbing. We find 55 species in Malaya and over 100 in New Guinea. A new revision of the 112 species claimed for the Philippines is a good starting point for the species in the eastern parts of tropical Asia¹¹.

CHASSALIA. [Commemorates, Antoine Chazal, 18th century French artist, botanical illustrator; the admittedly incorrect spelling is the accepted form.] This is a Paleotropical genus of about 42 species, some African and especially Madagascar. In tropical Asia, the chief species is *Chassalia curviflora*, which together with closely related variants is found in almost every lowland forest of the Sundaic Region. These are small fleshy shrubs of the forest understorey. They bear thin membranous leaves, distinctive when reproductive by virtue of the terminal white fleshy inflorescence stalk and bright purple berries. The flower is a narrow tube, slightly curved in most species with a flash of yellow in the throat.

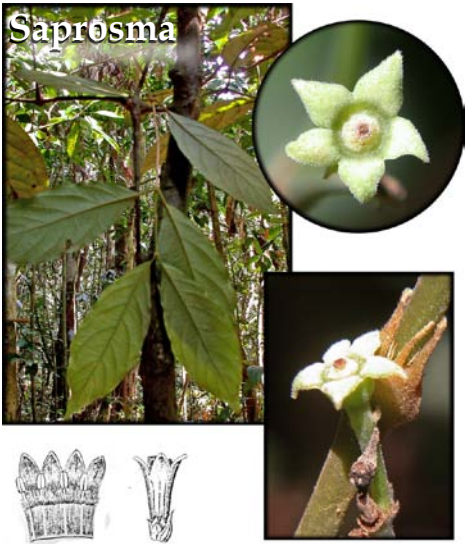
SAPROSMA. [Greek, rotten-smell.] A genus of about 30 species found throughout tropical Asia. *Saprosma* species are hard wooded trees of small to modest stature and as the name implies, the leaves do indeed have a nasty rotten sulfurous odor. A few other Rubiaceae are similarly malodorous, e.g., *Amaracarpus*, and the odd climber *Paedaria*. The flowers of *Saprosma* are small open and star-shaped from axillary clusters, the fruit



Psychotria. 1-2, *P. griffithii*, Malaya, a diminutive and arching understorey shrub, usually less than 1 cm DBH, with a sparse inflorescence of tiny flowers; 3, *P. ????* from Mt. Matalingham, Palawan, Philippines, with blue fruit; 4, *P. amplissima*, Luzon, Philippines, dense infructescence of red fruit; 5-7, *P. viridifolia*, from Sarawak, a broadly conceived and widespread species with a large open inflorescence of small flowers, the leaves dry dark red, the fruit barrel-shaped and strongly ribbed in a fashion characteristic of the genus. (Photographs 3 & 4 © Leonardo L. Co.)



Chassalia curviflora, Malaya, with characteristic terminal inflorescence of dense flowers, curved floral tube, yellow throat, purple fruit on white stalk.



Saproosma. photographs of *S. arboreum*, 4 cm DBH tree, Malaya, leaves (foetid odor), and flower; line drawing of corolla from BALLION *loc. cit.*

blue and black. The floral features seem to overlap with *Lasianthus*. Vegetatively they differ in their white angular twigs; the twigs are not strongly plagiotropic with numerous leaf pairs and the nerves are not so characteristically regular and arched as in *Lasianthus*, but these differences may apply only to the common species.

A - Tribe Lasiantheae - a

LASIANTHUS. [Greek, woolly-anthers.] Maybe 170 species, small shrubs common in lowland forest from tropical Africa to India, Taiwan and Australia. Malaya has 54 species, at least that many in Borneo, the Philippines about 20 species, Australia one. The genus is also abundant in the forests of Taiwan. *Lasianthus* species are common and abundant small trees of the dark forest understory. The most notable of their distinctive features is the asymmetry of the branching. Typically they bear a single upright axis with lateral plagiotropic branches. Although the leaves of the upright axis are arranged in distichy as is normal for Rubiaceae, only one of the axillary branches develops. The leaves of the lateral branch are arrayed in a horizontal plane. The venation is distinctive:

¹¹Sohmer, S. *et al.* 2007. The genus *Psychotria* (Rubiaceae) in the Philippine Archipelago. Botanical Research Institute of Texas.

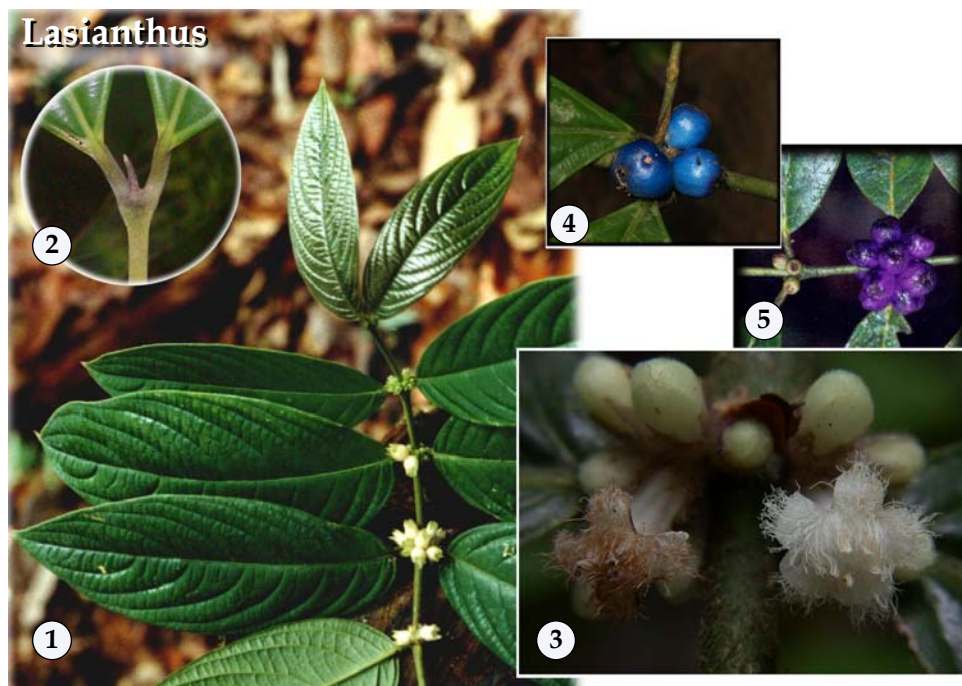
nerves are well-spaced and arching while the veins are regularly scalariform at right angle to the midrib. The stipules are variable, sometimes little more than a small flange of tissue, but in some species larger and inflated. The flowers are borne in dense, sessile, axillary clusters, the corolla a short white tube, the berries often a vivid blue, but also violet.

The genus is notable for the large number of poorly known or otherwise localized species. Not many are widespread, and more than a few are known from only a single locale, often only from the type and yet where they occur they might be one of the most abundant small trees. They are often in fruit even when nothing else is, and so may well serve as a critical food for understory birds.

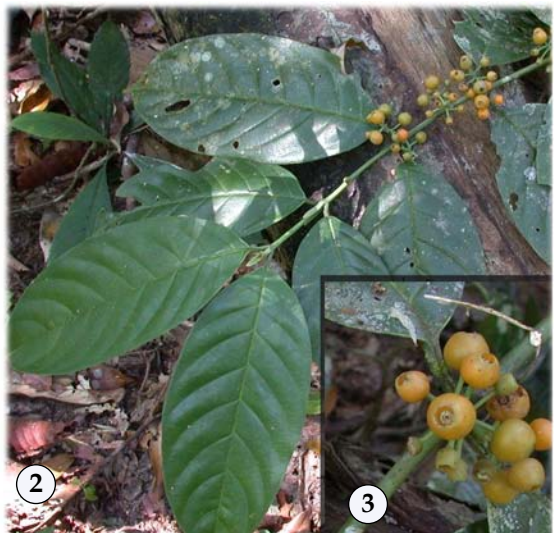
AMARACARPUS. [Greek, persistent fruit?] Monotypic, *Amaracarpus pubescens*, a stinky small shrub, of sparse and scattered distribution. It is found widely in the Sundaic Region, reaches north to the Thai Peninsula; Elmer collected it in Mindanao. (Not illustrated.)

A - Tribe Urophyllae - a

Genera of the *Urophyllum* Tribe all share a similar habit of paired plagiotropic lateral branches



Lasianthus. 1, *L. densifolia*, Malaya, long thin branches with leaves in a plane, the blade showing the characteristic venation; 2, the apex with the small sharp stipule; 3, the flowers of an undescribed species of *Lasianthus*, from Pasoh Forest, Malaya; 2 & 4, unidentified *Lasianthus* from Matalingahan, Palawan, Philippines; 5, *L. fordii*, Lataan, Philippines. (Photographs 2 & 4, © Leonardo L. Co; photograph 5, © Nestor Bartolome.)



Urophyllum. 1, *U. congestifolium*, Malaya; 2-3, *U. glabrum*, Malaya.

from an upright main trunk; the leafy branches are long with leaves in a plane, the inflorescence in axillary clusters, the leaf blade with nerves regular and arched, the veins at right angle to the midrib. Molecular data indicates that *Urophyllum* is paraphyletic and appears to include *Maschalocorymbus*, *Pleiocarpidia*, *Praravinia*, and *Pravinaria*. The formal transfers have not yet been made, and so I list the segregate genera here¹².

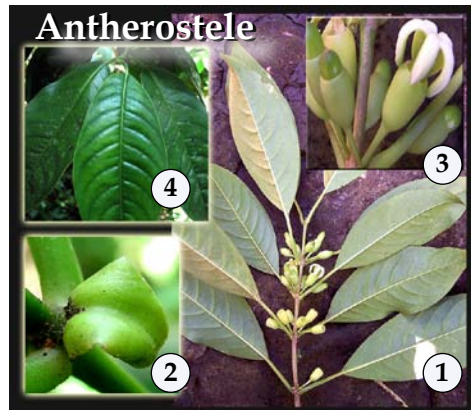
UROPHYLLUM. [Greek, tailed-leaves, in reference to drip tips, which are not especially characteristic of the genus.] 200 species of the Paleotropics. The stipule is typically blunt and papery and falls away leaving a distinctive white scar. The axillary buds are often multiple and serial, the leaves without domatia. In floral form *Urophyllum* is characterized as follows: axillary inflorescences of crowded branched cymes, interfloral bracts and bracteoles present, the flowers are small, with parts in four–eight, actinomorphic, unisexual, heterostylous or homostylous, usually with a stout pedicel, the short calyx tube is cup-shaped with small lobes that persist in fruit; the corolla is broadly cup-shaped without a significant tube and less than one cm long, the stigma three–eight lobed, fruits are fleshy berries with numerous seeds.

Several species are abundant in any forest, these as small shrubs but also as lower story trees that exceed 10 or even 20 cm DBH. Within the large-scale forest plots, *Urophyllum* always displayed a wide dissemination, high recruitment and high mortality, and occasionally fast growth. These trees commonly in fruit. A few of the small-statured species are thought to reproduce clonally.

ANTHEROSTELE. [Greek, flower column.] Four species, endemic to the Philippines, possibly a clade distinguished by the more salverform corolla.

PLEIOCARPIDIA. [Greek, many fruits.] 27 species, Borneo, one in Mindanao and perhaps northward in the Philippines along the wet eastern coast. Differs in that the inflorescences is a series of spikes on a branched stalk; involucre bracts absent; flowers oddly with parts in sevens (sometimes in *Urophyllum*), the corolla lobes are lanceolate, the stigmas five–eight lobed. (Not illustrated.)

PRARAVINIA. [Uncertain.] 50 species, Sulawesi, Philippines (19 species), New Guinea and Borneo. Differs from most *Urophyllum* in that the corolla tube is pu-



Antherostele. 1-3, *A. banahaensis*, Luzon, (© Leonardo L. Co); 4, flower of *A. luzoniensis* (© Ulysses Ferreras).

¹²Smedmark, J. et al. 2008. Taxon 57: 24-32.



Praravinia. Leaf, stipule and stipule scar of an unidentified species from Palau, Philippines; inset the flower of *P. sablanensis*. (© Leonardo L. Co).

bescent outside and the corolla lobes linear-lanceolate, the ovary partly inferior.

☪ - Subfamily Cinchonoideae - ☪

Sometimes trees of large diameter, some abundant woody climbers (*Uncaria*), mostly entire stipules, mostly without raphides, variable arrangement of corolla lobes, placentas with numerous ovules, fruit mostly dry capsule, seeds numerous, often winged, heterostyly frequent, stylar pollen presentation rare.

A - Tribe Guettardeae - a

Although the family Rubiaceae is plagued with too many small genera, large genera are not necessarily better. In the *Guettarda* tribe we find in Asia several genera that are species-rich but not monophyletic¹². The names of many of these trees may change in the coming decade.

GUETTARDA. [Commemorates J. Guettard, French botanist, d. 1780.] As currently conceived, a polyphyletic genus of about 150 species. Our most common species is *Guettarda speciosa*, a small tree, widely

distributed along the Pacific tropical shores, and readily recognized by its habitat, the long curved night-blooming white flowers and the woody fruits dispersed by sea currents. It seems to prefer a rocky substrate and often grows on naked stone of either granite or limestone; evidently long-lived, the trunk sometimes exceeding 10 cm diameter, but never getting tall. It is the type species of the genus and allied with an otherwise Neotropical clade that bears bisexual flowers. The rest of the Asian representatives are dioecious and evidently more closely related to species of *Timonius* and *Antirhea*. As a group, they are most prevalent in Philippines, Sulawesi, New Guinea and the Pacific, with sparse representation westward in Malaya, and perhaps three-four species reaching Peninsular Thailand and southernmost Cambodia and Vietnam.

ANTIRHEA. [Greek, against-flow, in reference to use as styptic to stop bleeding.] A genus of shrubs or trees, 36 species (including *Guettardella*), Madagascar, tropical Asia to the Pacific, with perhaps a dozen or so in the Philippines but only *A. atropurpurea* in Malaya and not found beyond Peninsular Thailand. Evidently polyphyletic and likely interdigitated with *Timonius*. The inflorescences is axillary, flowers actinomorphic with parts in fours, unisexual and homostylous. (Not illustrated.)

¹²Achille, F., et al. 2006. Annals of the Missouri Botanical Garden 93: 103-121.



Guettarda speciosa, on exposed coral islands, Hundred Islands National Park, Luzon, Philippines.

TIMONIUS. [From an Amboina name.] 180 species, centered in eastern tropical Asia, with 14 species recorded for the Philippines then westward to the Indian Ocean and Sri Lanka (1), the Seychelles, and Mauritius, and also east to Australia. The Malay for the common ruderal species is *rentap*. The species have been thoroughly monographed for the region^{13,14}.

A broadly defined genus, dioecious with numerous locales that develop into pyrenes. Diverse when all species are considered and includes the very odd subgenus *Abbottia* which are hemi-epiphytic, starting life on branches of trees, dropping adventitious roots down and then ultimately developing as a free-standing tree. Of this type we seem to have only *T. appendiculatus* in the wet eastern forests of the Philippines from the southern Sierra Madres to Mindanao. The more typical *Timonius* species in our area are fast-growing sun-loving species abundant in secondary forests and gaps such as *T. wallichii* and *T. flavescens*. In these the leaves are silvery and silky below, the flowers are often abundant and found scattered on the ground below the tree.

DICHILANTHE. [Greek, two-lipped flower.] A strange genus of 2 species, *Dichilanthe zeylanica* in Sri Lanka and *D. borneensis* endemic to west Borneo. These are small trees, distinctive in the curved floral tube with asymmetric lips (2 + 3), the sheathing stipular collar, and a pair of stipules that subtends the terminal fruiting

cluster. [Not illustrated, but see the description by Puff *et al.*¹⁵.]

A - Tribe Hymenodictyoneae - a

HYMENODICTYON. [Greek, membrane-net.] 20 species, in tropical Africa and Madagascar, with one species. *Hymenodictyon orixense* (with extensive publications under the name *H. excelsum*) in Thailand and the Philippines, Lesser Sunda islands, perhaps farther east, especially along the coastline, reaching Langkawi (where the Malay name is *lepar*), but not in the lowland equatorial forests of the Sundaic Region. The long pendent spikes of small white flowers and the dry dehiscent capsules are well-illustrated in PUFF *loc. cit.* Sometimes as a low shrub, but also as a fairly large tree, to 30 m or more in height with a pale light timber exploited at least in India if not much elsewhere. The trees are distinguished by the papery leaves that turn reddish before falling, and the long leaf stalks.

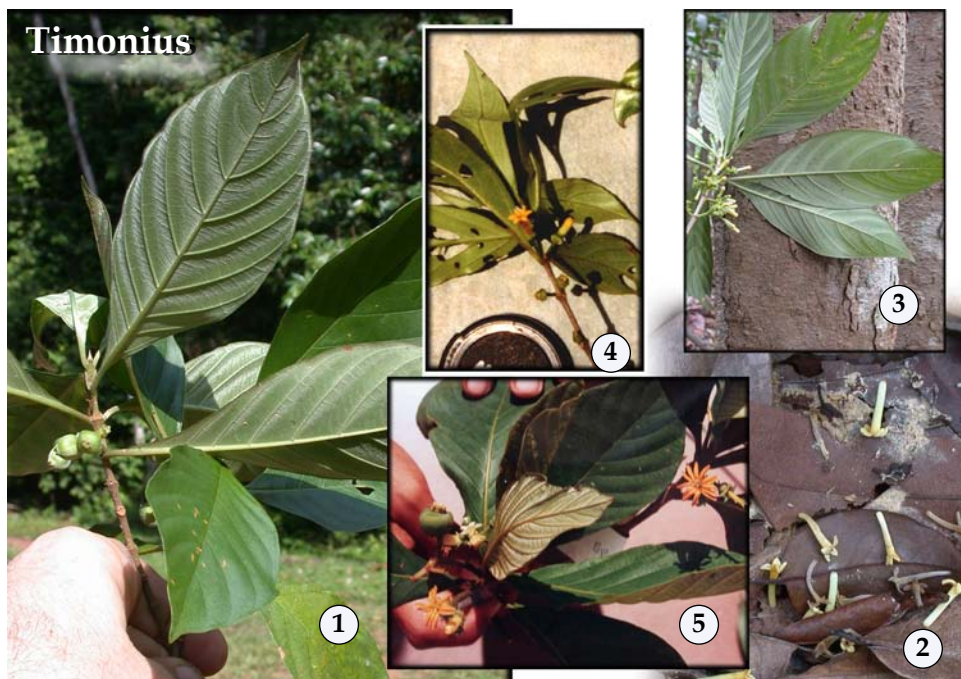
A - Tribe Naucleaceae - a

Medium and large trees and lianas with large stipules, thumb-nail-shaped or variously bifid. The

¹³Darwin, S. 1993. Allertonia 7: 1–39.

¹⁴Darwin, S. 1994. Systematic Botany Monographs. 12.

¹⁵Puff, C. *et al.* 1996. Nordic Journal of Botany. 16: 145 - 164.



Timonius. 1-3, *T. wallichii*; 1, in fruit, Malaya, the lower leaf surface is a silky silver; 2, in secondary forest in Singapore, the fallen flowers dense on the ground beneath the tree; 3, the trunk and flower clusters below the twig tip; 4, *T. ternifolius*, Sarawak, the corolla yellow; 5, *T. aff. stipulosus*, Sarawak, large-flowered, the fruit with a persistent crown of stipular lobes.

inflorescence is dense and globe-shaped, the flowers homostylous, corolla lobes imbricate in bud, while the fruit is either a fused syncarp, fleshy with numerous small seeds, or a mass of relatively free ovaries individually dehiscent. In geographic distribution, the *Nauclea* group is entirely Paleotropical with the exception of two species of the liana *Uncaria* in the American tropics and the shrub *Cephalanthus* in North America. The molecular data cited at the outset of this survey of the Rubiaceae indicates that *Hymenodyction* sits basal to the rest of the *Nauclea* group, sharing with them a Paleotropical distribution but differing in the spike of individual flowers rather than the globose heads. The most recent analysis of molecular data in the tribe identifies six main clades, five with strong support, and the most heterogeneous, the *Adina* group, with weak support¹⁶. The authors recommend the maintenance of no less than 22 genera. An outline of their arrangement is provided in the adjacent table and a student interested in the fine division of this group should begin with the cited article and the taxonomic papers referenced therein. The monographic studies by Colin Ridsdale are especially notable for their meticulous descriptions of individual species. Within the confines of the present volume, I will limit myself to a mention of only some of the more obvious and significant species, using the current standard name, but not otherwise noting the many genera. I might add that 18 of the 26 genera have only one to three species. As stated earlier: every clade needs a name, but not every clade need be a genus. While I do not specifically recommend lumping all 179 species under a single genus - such synonymizing should fall to the specialist - I would note here that too often in the Rubiaceae the concept of the tribe is used for what a botanist working on another family might call a genus. With fewer than 200 species, strong monophyly and a broad concordance of distinctive form, the *Nauclea* tribe could well be treated as a single genus that would be no more heterogeneous than *Dipterocarpus* and far less so than *Ficus*.

NAUCLEA. [Greek, little ship, probably in reference to the boat-shaped stipules.] The most common species is probably *Nauclea officianalis*. The Malay is *engkal* or *bengkal* with variants such as the Iban *jen-gkal*. Most species of *Nauclea* start to flower at a small size, but nonetheless continue to grow, with individuals sometimes reaching 50-80 cm DBH.

Genera of the Naucleaeae

Genus	Spp.	Distribution
Subtribe Naucleinae		
<i>Nauclea</i>	9	Afro-Asia
<i>Neolamarckia</i>	1	India eastwards to New guinea
<i>Sarcocephalus</i>	2	Africa (except northern)
<i>Burttavya</i>	1	East Africa
<i>Nauclea maingayi</i>	1	Suspected <i>Neolamarckia</i> - <i>Neonauclea</i> hybrid origin
Subtribe Adininae		
<i>Adina</i>	3	Asia
<i>Adinauclea</i>	1	Sulawesi
<i>Haldina</i>	1	Asia
<i>Metadina</i>	1	tropical Asia
<i>Pertusadina</i>	4	tropical Asia
<i>Sinoadina</i>	1	Asia
<i>Neonauclea</i>	65	tropical Asia
<i>Myrmeconauclea</i>	3	tropical Asia
<i>Ludekia</i>	2	Philippines, Borneo
<i>Diyaminauclea</i>	1	Sri Lanka
<i>Khasiaclunea</i>	1	India
Subtribe Breoniinae		
<i>Breonadia</i>	1	Afro-Madagascar
<i>Breonia</i>	20	Madagascar
<i>Gyrostipula</i>	2	Comoro Islands and Madagascar
<i>Janotia</i>	1	Madagascar
Subtribe Cephalanthinae		
<i>Cephalanthus</i>	6	Pan- and subtropical
Subtribe Mitragyninae		
<i>Mitragyna</i>	6	Africa, Asia
Subtribe Uncariinae		
<i>Uncaria</i>	34	Pantropical
Subtribe Corynantheinae		
<i>Corynanthe</i>	3	Central and West Africa
<i>Hallea</i>	3	Africa (except northern)
<i>Pausinystalia</i>	5	Central Africa

NEOLAMARCKIA. [Reference to J. Lamarck, d. 1829, French botanist and early evolutionist.] A single species for which the current preferred name is *Neolamarckia cadamba*; however, the species has appeared extensively under two other names: *Nauclea cadamba* and *Anthocephalus chinensis*. The name *kadamba*, or *kadam* is from Sanskrit; the Malay is *kelempayan* and was likely brought from Java; the Iban is *selimpoh* (not to be con-

¹⁶Razafimandimbison, S. et al. 2002. American Journal of Botany. 89:1027-1041.

fused with *simpoh*, the name for *Dillenia*), or *sempayan-bangkal* (Brunei), and *kaatoan-bangkal*, (Philippines). The timber is sold as *laran*, a name used at times for the tree. This is a well-known vigorous colonizer of logging tracks and secondary forest. The big leaves paired on the long horizontal branches are readily seen along roadsides of tropical Asia, although from a distance it can be easily confused with *Duabanga* (Sonneratiaceae); note that in the latter the new leaves are usually red. This is one of the few Rubiaceae that can grow to very large size. The branches abscise as a whole, even the very large branches in the mid canopy. The diameter growth rates are quite high in full sun on good soil; a tree can reach 70 cm DBH in under 30 years. Some plantations have been established in India and Sumatra, chiefly for matches or paper. The pre-human distribution in tropical Asia is unknown; it may be indigenous to some parts, and introduced in others. The *kadam* tree is mentioned in Sanskrit literature, and *kedam* inflorescences are garland and used in Hindu rituals. Certainly, it is likely that ancient Indian traders spread the tree to some degree within tropical Asia. The fruit head is fleshy at first and edible. The seeds and very small; seedlings are strong light demanders.

ADINA. [Greek, clustered, in reference to the flower in heads.] *Adina*, when treated narrowly, includes three species distributed from India to Myanmar, Thailand and Vietnam and sparsely southward. They are distinguished by the deeply divided stipules clustered at the terminal



Hymenodictyon orixense, large tree, the leaf stalk unusually long and slender for a Rubiaceae, the older leaves wither red; Bogor Botanic Gardens, Java.

bud, three to seven flowering heads per inflorescence, and four ovules per ovary. *Adina dissimilis* is small tree to 20 m, southern Thailand to Malaya. Similar genera and species include *Metadina trichotoma*, and perhaps four species of *Pertusadina*, especially *P. euryncha*, a large tree of lowland forest in the Sundaic Region; and *Haldina cordifolia*, a species found from Sri Lanka to Mainland SE Asia, just reaching the northern Malay Peninsula.

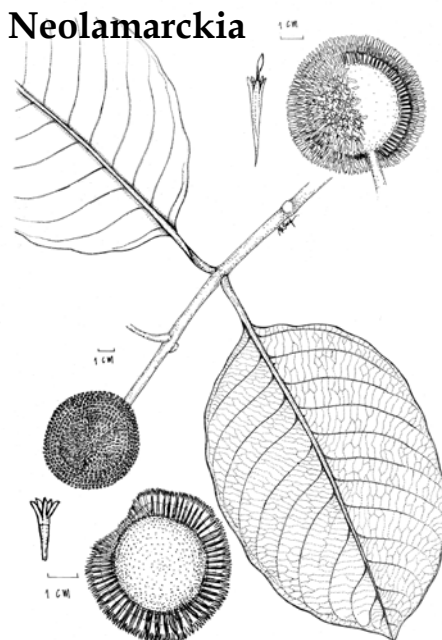


Nauclea officinalis; 1, the upper canopy of a mature tree, 44 cm DBH, Malaya, showing the characteristic arrangement of large lateral branches; 2-3, Philippines, the mature infructescence, compound, fleshy, indehiscent with tiny seeds. (Photograph 2, © Leonardo L. Co.)





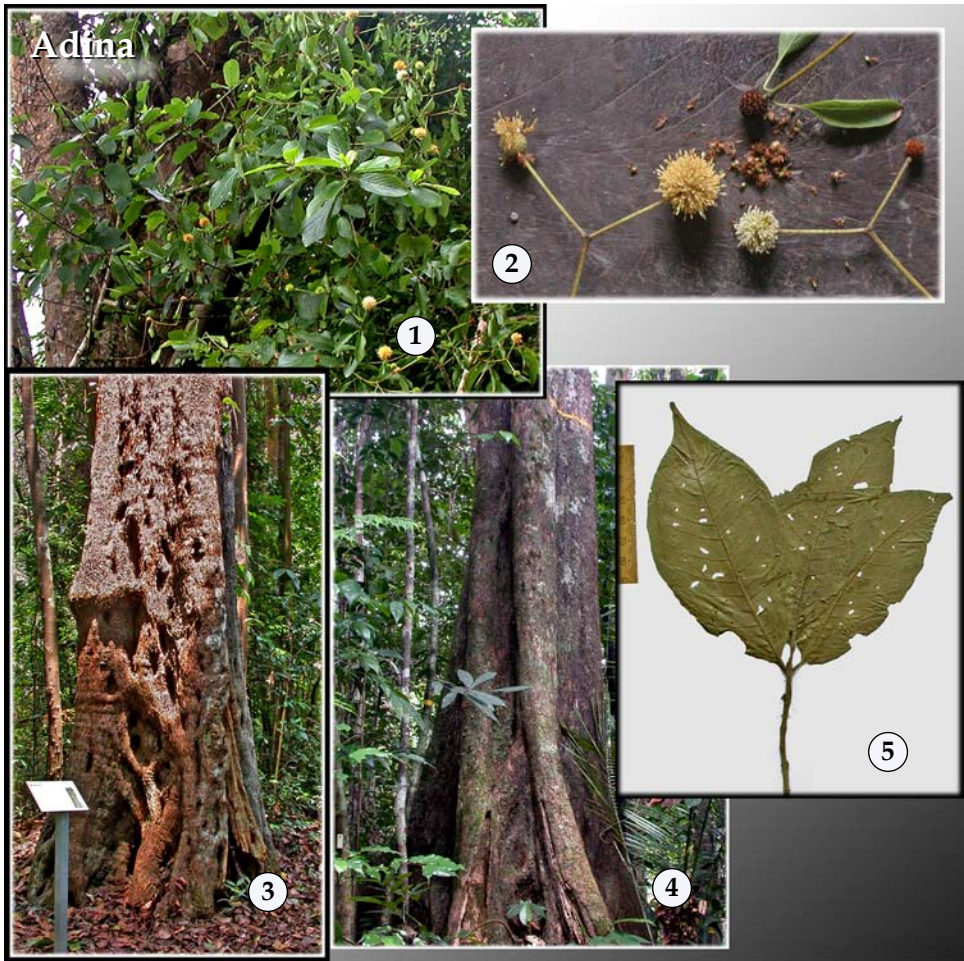
Neolamarckia cadamba, a large and isolated tree, 82 cm DBH, amidst mature canopy of Huai Kha Khaeng Wildlife Sanctuary, Thailand; saplings are found only far distant on forest margins and roadsides.



Neolamarckia cadamba, line drawing of leaves and twig, showing the small stipules, and inflorescence; the illustration is based on a specimen from the tree in the photograph to the left, from BU-NYAVECHEWIN *loc. cit.*



Neonauclea. 1-3, *N. calycina*, roadside Palawan, Philippines, note the large stipule; although the floral head looks distinctive, beware that more than 80 species of *Neonauclea* have been described and the floral heads of most look very similar to one another; 4-6, *N. gigantea*, Sarawak, a species with thickened ant-inhabited twigs.



1-2, *Adina dissimilis*, lakeside in the lowlands, southern Vietnam, terminal and axillary clusters of globose heads of flowers, each head about 2 cm across; the fruiting heads breaking up into individual dry and dehiscent fruits.; 3-5, *Pertusadina eurhyncha*; 3, Bukit Timah, Singapore; over 80 cm DBH, showing the typical latticed trunk of the mature tree; 4-5, Sarawak, 65 cm diameter above the buttresses, the lattice form is weak, the buttresses far more prominent; 5, a sterile voucher from Sarawak.

NEONAUCLEA. [Near to *Nauclea*.] A species-rich genus prevalent in Borneo, Sulawesi, and southern Philippines, and to some extent in Sumatra, but not in Malaya, Java or eastern Indonesia. Distinguished by the terminal inflorescences and free capsular fruits. Perhaps four species bear swollen internodes inhabited by ants (*Myrmeconauclea*), possibly a clade but likely nested within the more than 60 species of *Neonauclea*.

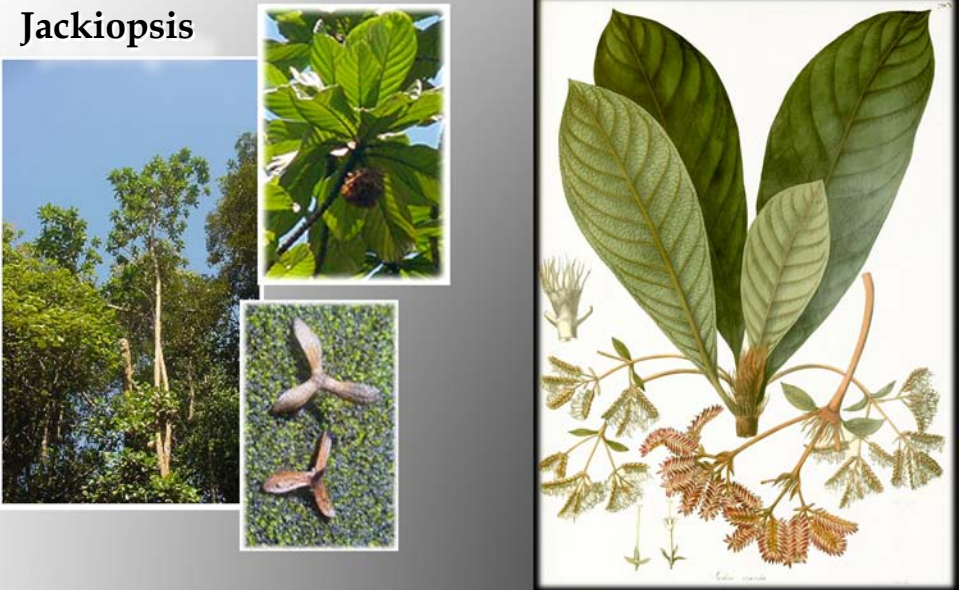
MITRAGYNA [Greek, in reference to the mitre-form stigma and ovary.] Differs in combination: corolla lobe valvate in bud, stigmas mitriform, numerous ovules basally attached. seven species of the Paleotropics. Known in Malaya as *ketum* or *kutum*. These are small to medium statured trees, the leaves ordinary and well-stalked, the stipules large and entire. The terminal inflorescences are without bracts, flowers bisexual, uniform,

five-parted, borne in globular heads, each carpel is free of its neighbors, and bears numerous ovules that develop into tiny winged weeds dispersed when the capsules split. The wings are small, the lower wing is bifid. I have a note that the leaves can be smoked as a narcotic.

A - Tribe Jackieae - a without subfamily

JACKIOPSIS. [Commemorates William Jack, Scottish botanist, resident of Penang, author of *Malayan Miscellanies*, d. 1822.] The singular swamp forest species, *Jackiopsis ornata*, is among the most easily recognized species of Rubiaceae in our region and yet it remains a mystery in almost respect. This is a fairly large tree. The stipules are unique in their deeply fringed margin, while

Jackiopsis



Jackiopsis ornata. On the left, photographs of a tall tree in the midst of a patch of swamp forest in Singaore; a dense inflorescence hangs beneath the clusters of leaves; the winged fruit; right, illustration showing flowers and details of the fringed stipule. (Photographs © Joseph Lai; illustration adapted from Wallich's *Plantae Asiaticae Rariores* of 1832.)

the winged fruit are peculiar as is the dense clustered inflorescence beneath the leaves that crowd the upright twigs. Never particularly abundant, but neither is it ever a surprise to find in permanently inundated forest. The basic biology is unknown as is the relationship of *Jackiopsis* to other Rubiaceae.

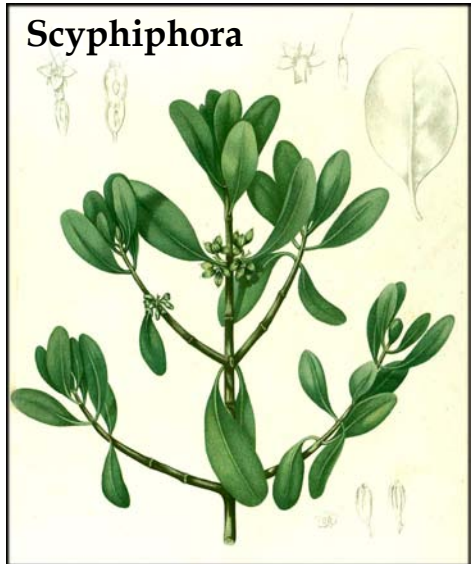
☪ - *Ixora* Subfamily - ☪ (Ixoroideae)

Mostly trees and multi-branched shrubs; stipules entire; usually without raphides; corolla lobes with contorted aestivation, placentas pluri-ovulate, seed number variable; typical fruit a fleshy berry (except *Gardenia* with a hard endocarp and numerous seeds); stylar pollen presentation general, flowers often unisexual.

A - Genera of Uncertain Placement a

WENDLANDIA. [Commemorates J. Wendland, German botanist.] 70 or more species, widely in Asia, typically shrubs and small trees of open sunny places in the dry-seasonal lands; not to be found in the shaded understory of the equatorial lowland forest. In most species the new leaves and the nerves are colored a dark red (at least in fresh specimens). The stipules tend to be ear-shaped flanges that stick out perpendicular to the stem and are inserted somewhat above the node. The indi-

Scyphiphora



Scyphiphora hydrophyllacea, a mangrove shrub, illustration adapted from BLANCO *loc. cit.*, Plate 277.

vidual species are evidently variable and not well-known. The fruit are dry capsules, the seeds small and numerous. These are pretty shrubs in flower and could be easily cultivated.



Wendlandia. Left, the red veins of the leaf, typical of the genus; center and right, *W. glabrata*, Cordillera of N Luzon, Philippines, about 1200 m elevation, showing the habit as a small tree, the spreading stipule and the flower. (Photograph on the left © Leonardo L. Co.)

SCYPHIPHORA. [Greek, a two-handled cup, maybe in reference to the spread stigma] A single species, *S. hydrophyllacea* of mangroves from India to Australia and the Solomon Islands. The Malaya is *chengam*. Merrill suggested that the city of Manila takes its name from the Tagalog *nilad* or *nilar*, Manila translating as the place where *nilad* grows. The stipules form a low cup-like rim with a slight fringe. The apex is protected by a resinous exudate. The flowers are basically similar to *Ixora*, the stigma is two-lobed and remains closed until after the anthers have wilted and reflexed away from the corolla's opening. The lobes then spread to expose the receptive inner surface. four-five merous, actinomorphic, bisexual, homostylous, Ovary bilocular, placentation axile, numerous ovules per locule; fruits fleshy, seeds two per locule.

GARDENIOPSIS. [Greek, like *Gardenia*, which it is not.] The single odd species *Gardeniopsis longifolia* from Malaya, Sumatra and Borneo. Easily recognized from the shiny resinous leaves with peculiar venation, and the long stiff terminal stipule. The species evidently of an isolated phylogenetic position. It is most always a small tree of the forest understory, slow growing with a maximum size of less than 10 cm DBH. In general, it seems to be a species that prefers wet ground and rich soils. In Lambir, Sarawak, it was found exclusively in a small wet patch over rich shale soils. It is not recorded from Kinabalu. At the Pasoh plot in Malaya, only two trees were found, both in standing water, but the species was common outside the plot in swampy ground. However, elsewhere in Malaya it is recorded with a broader ecology, from all provinces, from lowlands to lower hills.

It would be interesting to know more about this strange small tree.

A - Tribe Condamineae a

The three native genera included here are distinguished by the dry capsular fruit with a persistent calyx. They are chiefly medium or small trees. The molecular studies cited show, somewhat surprisingly, that at least *Mussaendopsis* (the only sequenced genus) falls into a strongly supported clade of Neotropical Rubiaceae that include *Calycophyllum* and *Warszewiczia*. The other two genera may prove unrelated.

MUSSAENDOPSIS. [Greek, resembling *Mussaenda*.] Maybe three species, the most widespread is *Mussaendopsis beccariana*, a large tree of lowland swampy forest gaps in the Sundaic Region. Also a newly described small shrub, *M. malayana*, from Gunung Tahan, and *M. celebica* from S Sulawesi. The fallen leaf can be confused with species of the *Nauclea* group, but the tree differs in the pale bole and of course the dry fruits with winged seeds are unique among Rubiaceae of the equatorial Asian forest.

DOLICHOLOBIUM. [Greek, long lobe or pod.] Probably fewer than 15 species, mainly in New Guinea and the Pacific Islands with *D. philippinensis* in the Philippines. A small tree, thin papery leaves, axillary inflorescences, flowers actinomorphic, bisexual, stamens inserted around middle (one/four-three/four of corolla tube),



Gardeniopsis longifolia; left, with floral buds, Malaya; right, dry leaf sample from Sarawak, showing peculiar venation and stiff long pointed pair of stipules at the twig apex.

ovules number two per locule, not pendulous. The seeds are winged.

GREENIOPSIS. [Greek, like *Greenea*.] Endemic to Philippines where Merrill named six species, and Elmer added a seventh. The most common is *G. multiflora*. Trees, two–10 m high, blade membranous or papery, Inflorescences present, terminal, Corolla campanulate or tubular, less than one cm long; stamens inserted in the distal one/four of the corolla tube.

A - Tribe Mussaendeae a

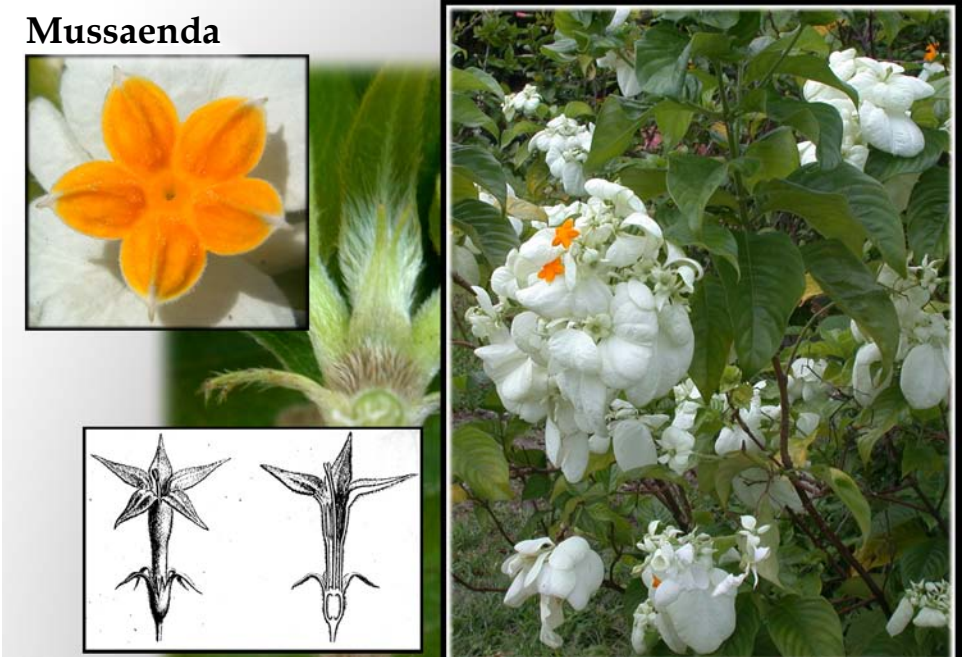
MUSSAENDA. [From a vernacular name for *M. frondosa* in Sri Lanka.] A strongly monophyletic group of seven genera and 170 species, Africa to Asia; without morphological synapomorphy but characterized by Alejandro *et al.*¹⁷ as bearing in combination “bifid stipules, shaggy trichomes, terminal inflorescences, heterostyly, semaphylls, corolla lobes with tail-like projections, discoid placentae, and fruits with tanniniferous idioblasts.” The authors prefer a seven genera system, with *Mussaenda* itself limited to 132 species, 97 chiefly in the dry-seasonal parts of tropical Asia and 35 species in mainland Africa, with six other small genera also of the Paleotropics. These small trees and scramblers are not to be found in the forest understory of the equato-



Mussaendopsis beccariana, lowland swampy forest in Malaya, 32 cm DBH with low buttresses; inset above shows the fallen leaves; inset below a mounted specimen from Sarawak, the infructescence with dehiscent fruit.

¹⁷Alejandro, G. *et al.* 2005. American Journal of Botany. 92:544-557.

Mussaenda



A cultivated form of *Mussaenda philippica*, native to the Philippines, flower, center background shows the stipule with a split tip; right, habit showing the large white calyx lobes, drawing of dissected flower. (Drawing adapted from BAILLON *loc. cit.*)

rial forests of the Sundaic Region. They include various habits from shrubs to small trees or lianas. The calyx is famously variable in the extent of the lobing which can be uniformly short, to unequally foliaceous, or all developed as conspicuous colored bracts, especially in the widely cultivated forms of *M. philippica*. The fruits are fleshy, indehiscent berries, characteristically warty, with numerous seeds. I should mention two Borneo shrubs in the related genus *Neomussaenda*, *N. xanthophytoides*, which was transferred from *Greenea xanthophytoides*, and *N. kostermansiana*. These species are little known, and were not included in the molecular study. Also note that the genus *Mussaendopsis* bears no close relation to *Mussaenda* despite the name.

A - Tribe Vanguerieae - a

The four genera listed here represent the predominantly Paleotropical tribe Vanguerieae that has been plagued by questions of monophyly. The work of Diane Bridson at Kew began the reorganization of the genera, and recent molecular work has only confirmed the wide polyphyly within the group. However, both the monographic and molecular work has focused on the African species^{18,19}.

MEYNA. [From an Indian name.] Eleven species of thorny trees, from tropical Africa and India, especially *Meyna laxiflora* of India; with three species in dry deciduous forests of Mainland SE Asia as far south as Langkawi, but not farther east.

PERAKANTHUS. [In reference to its home in Perak State in Peninsular Malaysia.] *Perakanthus velutinus* is apparently the only valid species; a second name by Ridley was in error. A small shrub to four m tall, endemic to Malaya; vegetatively indistinguished from *Psydrax*.

PSYDRAX. [Greek, warty in reference to the fruit of some species.] Maybe 30 or species in tropical Asia, allied with an uncertain number to the west as far as Africa. Most of our species are still recorded in regional literature as *Canthium*, and although that genus is now restricted to small spiny trees of Africa, the species of tropical Asia have yet to be transferred to another genus, *Psydrax* or otherwise. A regional monograph will likely see the creation of new genera to accommodate the diversity of form. Most all our trees are recognized by the paired glossy leaves ranked along horizontal branches, the blades with a few weak arching nerves, the inflorescences are axillary umbel-like clusters of white flowers that yield small green berries. The Malay names of *tulang-tulang* and *tulang ular*, while the Iban is generally *janang*.

¹⁸Lantz, H. *et al.* 2004. Botanical Journal of the Linnean Society. 146: 257–283.

¹⁹Puff, C. *et al.* 2005. Sandakania. 16: 29–47.



Psydrax. The species are described under the genus name *Canthium* because new combinations under *Psydrax* have not yet been made. 1-2, *Canthium monstrosum*, Philippines; 3-4, *Canthium gynochthodes*, Philippines; 5, *Canthium* Malaya; 6, *C. pedunculare*, Philippines. (Photograph 1, 2, 3, 6 © Leonardo L. Co; photograph 4 © Nestor Bartolome.)

A - Greenea Group - a

ALEISANTHIA. [Greek, bowl-flowers, probably in reference to the bowl-like fruit.] Two species, Malay Peninsula, *A. sylvatica*, a four m tall tree only from type locality in Kelantan, and once collected as a one m shrub at Klang Gates. These tiny shrubs were described by Ridley more than 70 years ago, and no new species have been found since, which must surely be an oversight of collecting. They are distinguished from all other Rubiaceae by the extremely dense coat of white woolly hair on the lower surface, and by the odd fruit which dry and split into two halves. (Not illustrated.)

GREENEA. [Commemorates American Benjamin Greene, d. 1862, botanist of Western North America.] Maybe seven species, *G. corymbosa* is widespread from Peninsular Thailand and Vietnam to Malaya, ? Borneo and only *G. hirsuta* is claimed for the Philippines. The small shrubs are immediately distinguished when in flower by the terminal inflorescence with individual floral branches that are scorpoid, that is, arched like a scorpion's tail with the flowers all on the convex side and opening singly from the tip downward. The flowers are small, compact, whit, bisexual and otherwise undistinguished, while the fruit are dry capsules that split to disperse the many small dry seeds. (Not illustrated.)

A - Tribe Ixoreae - a

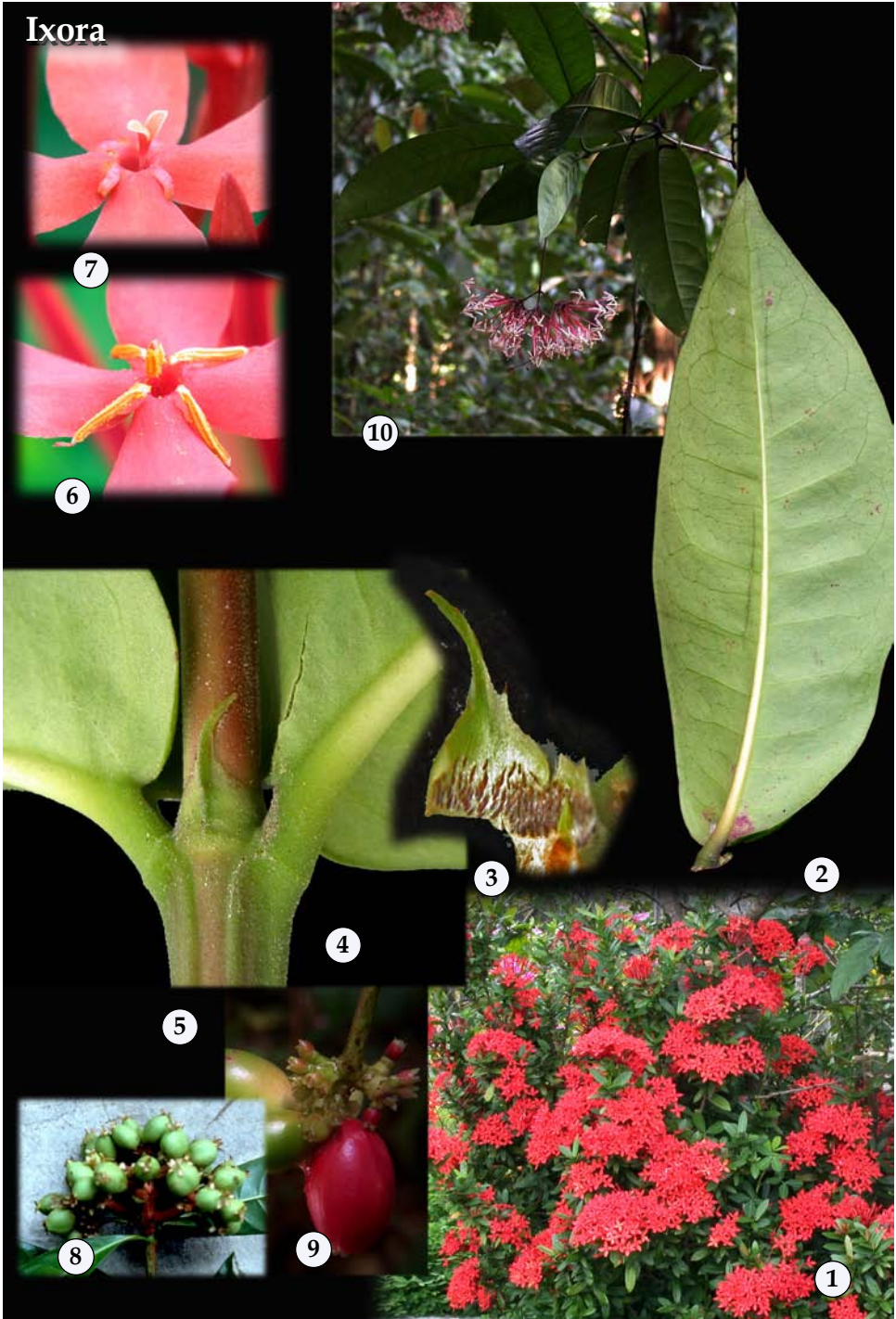
IXORA. [Sanskrit: Icvara, supposedly after 'iswara' a god of Malabar people to whom flowers of some species were offered.] 500 species, Paleotropical. The cultivated and forest species are usually recognized by the same common names: *pecah periok* in Malay, *gergansi* in Iban, and in the Philippines generally as *siantan* or *santan*.

Mouly *et al.*²⁰ found that *Ixora* comprises three main geographically defined clades across Africa, Madagascar and Asia. *Ixora* is paraphyletic with respect to the several segregate genera, and they propose a broad circumscription to include *Captaincookia*, *Doricera*, *Hitoa*, *Myonima*, *Sideroxyloides*, *Thouarsiora*, and *Versteegia*.

These are variously as multi-branched shrubs, small trees and a few medium trees exceeding 10 cm DBH. Twigs are terete with a cluster of leafless nodes marked by the persistent stipules which end in a long stiff needle-like tip. These are among the most abundant species of the family in lowland and mid-montane forests. Although the majority of species have red flowers; white and yellow are also known. Species from India to the Sundaic Region bear their flowers in terminal inflorescences; a few cauliflorous types are found in the easternmost part of Asia including New Guinea and New Caledonia.

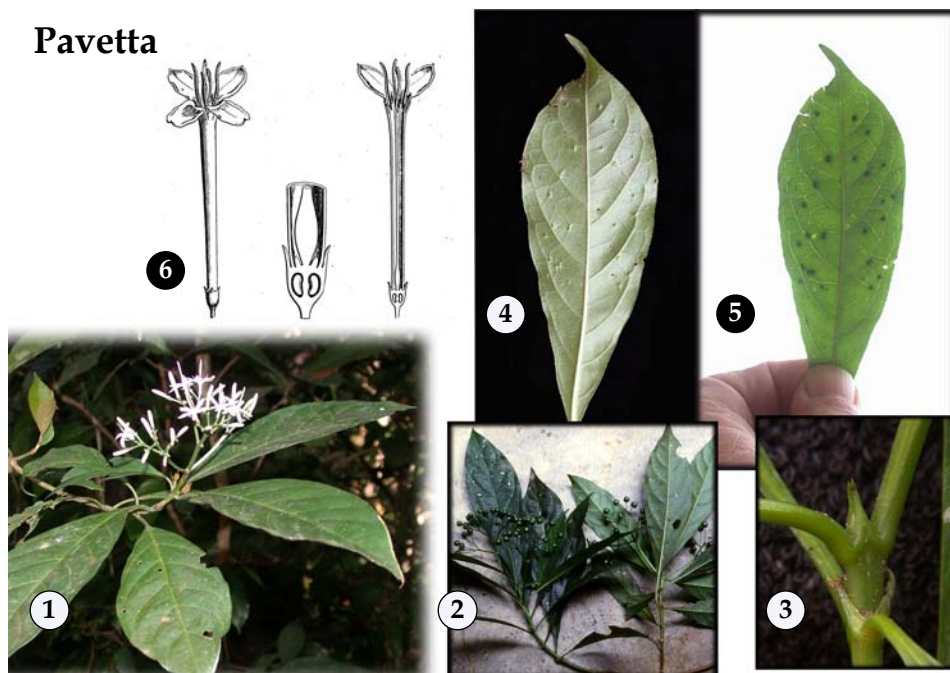
Ixora coccinea may be the most widely cultivated shrub in Asia. It makes a dense hedge with more or less continuously produced flowers, but rarely (never ?) setting fruit. The flowers bear parts in either fours or fives; each ultimate branch consists of a terminal flower, and two lateral flowers axillary from the scale leaves below. The lower flowers are usually in fours, while the ter-

²⁰Mouly, A. *et al.* 2009. American Journal of Botany. 96: 686-706.



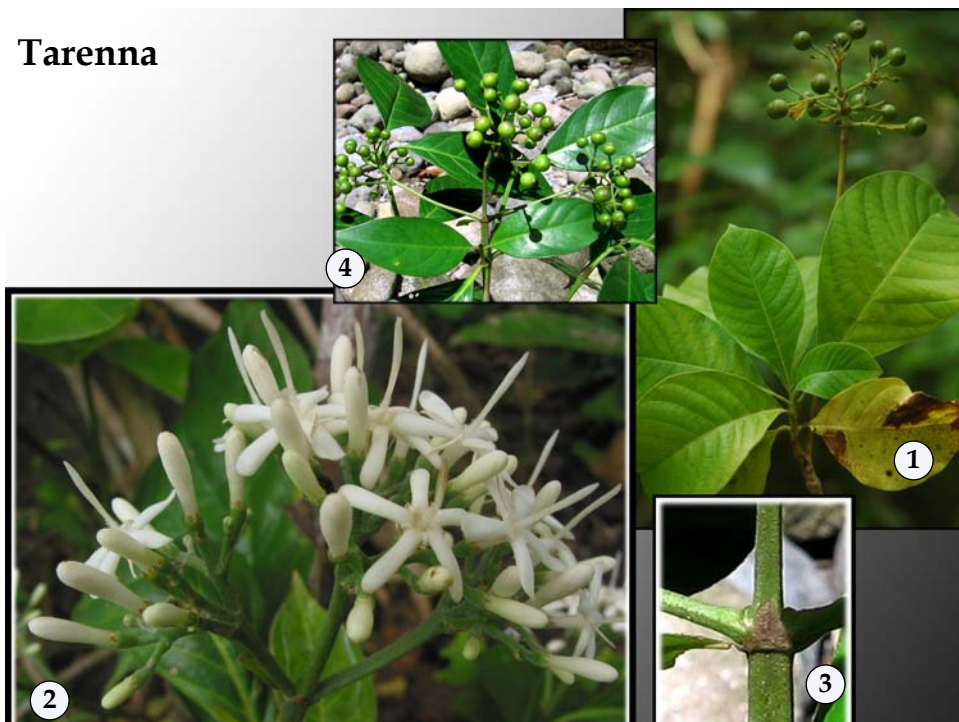
Ixora. 1-7, *I. coccinea*, cultivated in the Philippines; 1, habit; 2, leaf showing venation; 3, the inside of the leaf base showing the black glandular colleters; 4, node showing the stipule, keeled with an extended awned apex; 5, twig with characteristic congested cluster of old stipules; 6, flower showing the reflexed anthers at anthesis; 7, flower after anthesis, the receptive stylar lobes spread; 8, infructescence of *I. lobbii*, Malaya; 9, individual fruit of *I. pendula*; 10, the pendant inflorescence of *I. pendula*, the form in Malaya with long inflorescence stalk and flowers flushed with white and red.

Pavetta



Pavetta. 1, *Pavetta* 'Makiling'; 2, an undescribed species of *Pavetta* from Malaya; 3, typical stipule; 4-5, the leaf nodules that characterize the genus; 6, *P. indica*, line drawings from BAILLON, *loc. cit.*

Tarenna



Tarenna. 1. *T. arborea*, Hundred Islands, Philippines; 2-3, unidentified species, 2, from Palau, Philippines; 3-4, from Bataan, Philippines, note the square stem and simple triangular stipule. (Photographs 1 & 2 © Leonardo L. Co; photographs 3-4 © Ulysses Fer-

minal flower bears parts in fives. *Ixora javanica* is also widely cultivated for the large leaves and flowers. It has a more coarse and robust appearance. *Ixora pendula* is a treelet of modest size of the lowlands and lower hills of Malaya; when a tree of 5-8 cm DBH is in full flower, it is a remarkable sight. The flowers, white with a red flush at the throat, are borne in dense clusters typical of the genus, but they hang below the branches like ornaments. Not all races are equally attractive: those borne on long stalks and with the best color should be brought into cultivation.

A - Tribe Pavetteae - a

PAVETTA. [From a Sinhalese name.] 400 species, centered in Africa, but also rich in Asia from India to Borneo. The most common Malay name is *jaram-jaram*. *Pavetta* is readily recognized in tropical Asia by the conspicuous leaf nodules. Little definite information exists on the physiology and the benefits conferred by these bacterial nodules. In appearance, they are often more deeply green than the surrounding tissue, and the presumption of nitrogen fixation has never been demonstrated unequivocally. Plants grown without the bacteria typically develop malformed leaves, and eventually die, leading to the suggestion that the bacteria provide a plant hormone, lost from the host plant.

Species of *Pavetta* are often abundant shrubs in lowland and low elevation hill forests, often conspicuous with their great white inflorescences flowering in synchrony. The leaves are often smooth and papery as in *P. indica* but in *P. tomentosa* (abundant in lower mountain forests in the northern parts of Mainland SE Asia) they are densely hairy while those of *P. asper* are very rough to the touch.

TARENNA. [From a Sri Lankan name.] A species-rich Paleotropical genus with 300-400 species, perhaps equally divided between Africa and Asia with about 17 species in China, 35 in Mainland SE Asia, about 40 in Malaya, nearly half without names, about the same situation in Borneo and at least 20 in the Philippines. Obviously the genus needs a complete revision for Asia. The Malay is *nyarum hutan*. Many of our species bear silky hairs on the lower side and perhaps a majority have a twig that is square in cross-section.

A - Tribe Gardenieae - a

Gardenia and associated genera form an exceedingly messy group of more than 70 genera, well over 1000 species, of pantropical distribution, and an admittedly paraphyletic/polyphyletic structure. This tribe continues to resist clarification, and should a highly supported phylogeny be uncovered, there is every possibility that the resulting genera will lack simple diagnostic characters. Most of the morphological details used to segregate genera in

the past, such as pollen in monads versus tetrads, appear non-homologous in molecular studies. The tribe includes not only the important ornamental cultivated species in *Gardenia* but also a variety of other ecologically important trees in Asia. Wong Khoo Meng has analyzed the genera within the Malayan region²². The group as a whole shows a strong propensity for anisophylly. In some species we find one of a pair of leaves reduced to a stump (*Aidia*) in others they are simply unequal (*Porterandia anisophyllea*) while in yet others we find a normal leaf pair brought adjacent to an unequal pair by a shortened internode and so appearing to bear leaves in threes (some *Rothmannia*).

GARDENIA. [Commemorates Alexander Garden, English-born American naturalist, d. 1791.] I would include within *Gardenia* the Thai rheophytes often named under *Kailarsenia*. A genus with perhaps 60 species, of the dry-seasonal Paleotropics, more than 10 in Thailand, six in Malaya, four in the Philippines. *Gardenia* species are most prevalent in dry seasonal forests and rarely abundant in the everwet equatorial forests. The Malay is *mentiong*, Iban is *malau*.

The leaves are variable but often bear domatia in the nerve axils, while the stipules typically form a closed tube. The apical bud of many species is resinous. The calyx is fused throughout most of its length and ornamented with five ribs.

The most abundant cultivated species is known to horticulture as *G. jasminoides* or the Double-Gardenia. This is not the jasmine flower, which comes from an unrelated climbing plant. In the Philippines this is called *rizal*. The beautiful white flowers of this common shrub exude their familiar fragrance at most times of the day, but this becomes especially strong in the early evening. *G. coronaria* with hairy leaves, to 15 m, abundant tree of dry open forests Thailand, Myanmar and Indochina.

In the lowland equatorial everwet forests, the genus is sparse, and chiefly of larger trees of wet ground. *Gardenia pterocalyx* is found in Sarawak swamps (*malau paya*), while *G. tubifera* is a large tree of variable leaf form, from Thailand throughout the Sundaic Region. The fruit, up to five cm across is remarkable within the family: the outer wall splits and spreads back and away from the fruit, while a hard bony inner wall breaks into five to seven parts that spread not quite fully, and holds for display a mass of seeds embedded in a bright red pulp.

CATUNAREGAM. [From the Indian name.] About eight species from Africa and India to Mainland SE Asia. Especially *Catunaregam spinosa* (formerly *Randia spinosa*)

ROTHMANNIA. [Commemorates G. Rothman, Swedish botanist, d. 1778.] Taken as a broadly Paleotropical genus of about 40 species, *Rothmannia* is doubtfully monophyletic. The name is based on an African species and its near relatives. In Asia, the species

²¹Persson, C. 2000. Nordic Journal of Botany. 20: 257-269.

²²Wong, K. 1984. Malayan Nature Journal 38: 1-57.



Gardenia. 1, *G. merillii*. Sta. Cruz, Philippines; 2, commonly cultivated in the Philippines, increasingly popular in the tropical world, intensely fragrant, this small shrub is usually called *G. carinata*, (the type from India) or *G. coronaria* (the type from Burma), and wrongly in horticulture as Malayan *Gardenia*, it would be good to know more of its origin and spread; 3-5, *G. rubiflora*, Pasoh, Malaya, a large forest tree, the fruit with a hard endocarp that splits and spreads to hold the seeds and red sweet mass; 6, longitudinal diafram of the flower. (Photograph 1, © Leonardo L. Co; drawing from BAILLON *loc. cit.*)

assigned here number about 18, from India and Mainland SE Asia eastward to Borneo. The Thai tree, *R. wittii*, is common in deciduous forests. The diminutive *R.*

macrophylla of Malaya bears an exceedingly large flower and leaves that are strictly paired. The other species illustrated, is usually known as *R. malayana*, but much older and widely used names are *Gardenia grandis* and *Randia grandis*, but the transfer of the epithet is yet to be made. This tree has the leaf arrangement most typical of the genus wherein a pair of leaves above a long internode is followed by a very short node and a completely anisophyllous leaf pair such that the node appears to have three leaves in a whorl.



Catunaregam spinosa, cultivated in Bogor Botanic Gardens.

PORTERANDIA. [Commemorates G. Porter, early chief of Penang Botanical Garden.] Usually treated as 22 species, centered in Borneo and not found much outside the everwet evergreen forests. *Porterandia anisophyllea* is one of the more abundant gap plants of forests in the Sundaic Region; the Malay is *tinjau belukar*. At maturity the leaves are in strongly unequal pairs; the thick white flowers clustered below the upturned rosettes of leaves. It is edaphically broad, tolerant of wet and dry ground from lowlands to mid elevations. However note that there are numerous other species and most are superficially similar to one another. The genus has been recently revised.

AIDIA. [Greek, long-lasting, in reference to the wood.] 18 species, Africa, Asia and Pacific. Most species, perhaps all, with leaves arrayed in a plane, one leaf of each



Rothmannia. Left and inset, *R. macrophylla*, small shrub in Pasoh, Malaya, with paired 'rabbit-ear' leaves; right, specimen from Lambir with leaves in threes, locally known as *Randia grandis*, yet to be transferred to *Rothmannia*.

pair reduced to a scale. *Aidia wallichiana* is an abundant small tree of the lowland Sunda Shelf forest.

Sarawak which was Ridley's *Tarenna axilaris*. (Not illustrated.)

TAMILNADIA. [After the Indian State of origin.] Monotypic segregate of *Gardenia*, *T. uliginosa*, of India and Mainland SE Asia. (Not illustrated.)

KOCHUMMENIA. [Commemorates KM Kochummen, b. 1931, Forest Botanist of Malaya.] Three species of small shrubs rarely collected in Malayan forests. Close to *Rothmannia*.

CERISCOIDES. [Resembling *Randia* section *Ceriscus*.] Seven species, India to Indochina, Malaya one (Perak, two 19th century collection). Spiny, the flowers on axillary shoots, the ovules are one-celled, with many parietal ovules. (Not illustrated.)

FAGERLINDIA. [Commemorates F. Fagerlind, b. 1907, Swedish botanist.] Six species from India to Mainland SE Asia. The most abundant is probably the small spiny shrub *Fagerlindia fasciculata*, which reaches as far south as northern Malaya. (Not illustrated.)

TARENNOIDEA. [Greek, allied with *Tarenna*.] Probably only *T. wallichii*, a common tree of seasonal Mainland SE Asia. A second species, *T. axillaris* is known only from the Haviland type specimen from Matang in



Porterandia anisophyllea, Pasoh, Malaya, unequal leaves, with fallen large leaf and fruit, white flowers below the leaves, the bark is typically grid-cracked.



Aidia wallichiana, Pasoh, Malaya, lower inset shows the bark of an 8 cm DBH tree; in alternate pairs of leaves one of the leaves is reduced to a awl-like scale, magnified in the upper inset.

BRACHYTOME. [Greek, a shallow-cut in reference to the shortly lobed calyx.] Four species, generally in India and eastward in wetter and semi-evergreen forests of southern Myanmar, Indochina and reaching northern Malaya and east Sumatra. The habit is similar to *Aidia* in that one leaf at a floral node is reduced to a scale, but the internode preceding flowering node is much shortened. (Not illustrated.)

DUPERREA. [Presumably named after 19th century French Admiral Guy-Victor Duppere.] Especially and maybe exclusively *D. pavettifolia*, found from India to S China and much of Mainland SE Asia. (Not illustrated.)

RANDIA. [Commemorates British botanist Isaac Rand.] Although the genus *Randia* is today regarded as strictly Neotropical, we need to mention the name because so many Asian species within the *Gardenia*-group were at one time or another named *Randia* and the name is everywhere in the literature and annotations of herbarium specimens. The Kew World Checklist can be consulted for the appropriate synonym if it is known, but there may be more than a few tropical Asian species still to be formally transferred from *Randia*.

A - Tribe Coffeae a

Paired leaves with axillary floral clusters, berry-like fruit with large seeds and a thin pulp.

COFFEA. [From the ancient word for the berry and drink.] *Coffea* is a genus of more than 40 species that are native to Africa and Madagascar, with two species cultivated everywhere in the tropical world, in home gardens and plantations. There is such a large literature concerning cultivated coffee that nothing is added here except to note that they abundantly cultivated in lowlands and mountains in Vietnam, Java and Sumatra and the Philippines.

DIPLOSPORA. [Greek, double-seed.] A small genus of nine or 10 species found from Sri Lanka to Mainland SE Asia (three species) eastward to the Philippines and the Pacific. *Diplospora* has a sister taxon in the very similar *Discospermum*. The pair were formerly placed near *Gardenia*, but molecular evidence clearly allies these common trees with *Coffea*, which is interesting in that they are widely known in Malay as *kopi hutan*, although that name is often tossed about broadly for any Rubiaceae with axillary flowers.

Diplospora malaccensis is medium-sized tree, widespread and common in lowland wet forests throughout tropical Asia. It is called the ivory tree or *gading-gading* in Malay, in reference to the hard strong wood. A few species are more narrowly distributed shrubs and trees of mountain-sides. The leaves often with domatia, stipules shortly sheathing, usually with a short awn, inflorescence axillary, many-flowered, congested. The flowers bear parts in fours, their sexuality can be male or bisexual, in a few species seem to bear unisexual flowers. *D. lasiantha* has a strong fetid odor. Fruit a small globose to ellipsoidal drupe, < 10 mm in diameter. The seeds number one to three per fruit, not embedded in placental outgrowths.

DISCOSPERMUM. [Greek, for the rounded seed.] A small genus of seven species, more or less overlapping with *Diplospora*. These are uncommon trees, chiefly of seasonally dry places. (Not illustrated.)

XANTONNEA. A genus of two species, *Xantonnea parvifolia* and *X. quocensis*, known by little more than the type collections, from Mainland SE Asia. Small trees, evidently similar to *Hypobathrum*. (Not illustrated.)

HYPOBATHRUM. [Greek, seated beneath, in reference to the two seeds one under the other.] Maybe 20 species of tropical Asia, formerly known by the much prettier name *Petunga*. These are common small trees of the lowland equatorial forests, distinguished by the long branches bearing pairs of leaves that lie flat in a plane, axillary spike-like inflorescences that arch upward, and a peculiar twisted stipule pair.

ZUCCARINIA. [Commemorates G. Zucharini, d. 1847, Professor of Botany at Munich.] Only *Zuccarinia macrophylla*, a strange and poorly known small tree, restricted to Java. In form, it is similar to *Hypobathrum*,



Coffea, cultivated in the lower mountains of northern Luzon, Philippines; the shrubs bloom synchronously in great profusion; the fruit ripen slowly.

but with huge leaves, 30 cm or more in length, and the inflorescence evidently condensed to stalked heads. (Not illustrated.)

☞ - Unplaced Genera - ☞

COPTOSAPELTA. [Greek, a combination of to cut and shield, in possible reference to the stump in the fruit after the seeds fall.] 13 or so species, of Asia from the Temperate Zone to the tropics. Mostly (?) lianas but they are not uncommon in secondary forests and sometimes grow as scrambling shrubs. In flower these look like ordinary Rubiaceae with a simple triangular stipule and a terminal branched inflorescence, spreading petals white or yellow, and exemplary secondary pollen presentation. But the ovary is odd in the two locules with numerous ovules, maturing as a small woody dehiscent capsule bearing slightly winged seeds.



Diplospora. Lower left, mature trunk of *D. malaccensis*, Pasoh Malaya; upper left, dry specimen of *D. beccariana*, Lambir Sarawak; upper right, the axillary clusters of fruit of *D. tinagoensis*, Philippines; lower right, a mature tree from Huai Kha Khaeng, Thailand. treated, perhaps wrongly, as *D. malaccensis*. (Photograph of *D. tinagoensis* © Leonardo L. Co.)



Hypobathrum racemosum, Pasoh, Malaya, with axillary spikes of flowers; below, specimen of the same showing the long stipule air at the twig apex, twisted.



Coptosapelta olaciformis, a sprawling and sometimes climbing shrub, Mt. Matalingham, Palawan, Philippines. (© Leonardo L. Co).

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ASTERIDS (LAMIIDS): GENTIANALES

GENTIANACEAE

NAME: From the genus of herbs, *Gentiana*. The gentian family is not well known in Asian tropics and has no common name.

OVERVIEW: The Gentianaceae are a roughly cosmopolitan family especially abundant as herbs in the North Temperate Zone and especially well known as classic cold weather wildflowers. It includes 87 genera and 1655 species. Most gentians are herbs with opposite, paired and nearly sessile leaves that are joined at the base; the blade glabrous with entire margins; the flowers large, bisexual, actinomorphic, with a pronounced persistent calyx with lobes fused at least at the base, the petals fused as a tube in the lower portion while the petal lobes twisted to the right in bud, the stamens inserted in the tube, a bicarpellate gynoecium is superior, the ovules with parietal placentation. The family is extensively described in a dedicated web site maintained by Professor Lena Struwe at Rutgers University¹.

Gentians are uncommon in tropical Asia. For example, other than *Fagraea*, the Philippines claims nine native genera and about 15 species, chiefly herbs of open wet grasslands in high mountains. Most books of Asian trees will list *Fagraea* as belonging in a heterogeneous Loganiaceae. The affinity with the Gentians is suggested by its chemical constituents (xanthones, special seco-iridoids, the absence of alkaloids), and molecular evidence (a large deletion in the *trnL* intron gene).

FAGRAEA. [Commemorates J. Fagraeus, Swedish naturalist, d. 1747.] *Fagraea* is a genus of about 70 species found exclusively in tropical Asia from India and Sri Lanka to southern China and east to Australia and the Pacific, with a center of diversity in Borneo where more than 40 species have been noted. The analysis by Wong Khoon Mheng and John Sugau² is the starting point for the modern study of the genus which has suffered in the past from excessive lumping. Most species are called *temasuk* or *tembusu* or some variant.

The genus include a diversity of habits that range from large trees to smaller shrubs, lianas, stranglers and many epiphytic shrubs. The leaves are opposite, somewhat fleshy with relatively weakly lignified nerves. The node is peculiar and important in details with regard to identification to species. The apex is typically hidden between the clasping leaf bases. At maturity, the node usually includes a scaly sheath, short or long, that sur-

¹Struwe, L. 2002-2008. Gentian Research Network. (<http://www.rci.rutgers.edu>).

²Wong, K. *et al.* 1996. Sandakania 8. 1-93.

³Motley, T. 2004. Economic Botany 58: 396-409.